

The animal cultures debate

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Recent interest in animal cultures has been fuelled by high-profile reports of intra- and interpopulation differences in the behavioural repertoires of primates and cetaceans, consistent with the existence of socially learned traditions. Several studies have mapped spatial differences in behaviour, revealing a mosaic of behavioural phenotypes within species. The dominant current approach attempts to determine whether this is cultural variation by excluding asocial learning, ecological or genetic factors. However, claims of animal cultures remain controversial because such comparisons are subject to weaknesses; thus, new approaches to isolating the influence of culture on behaviour are required. Here we suggest that, rather than attributing behaviour to explanatory categories, researchers would often be better advised to partition variance in behaviour to alternative sources.

Introduction

The 'inheritance of acquired behaviour' has been a long-standing interest of biologists and psychologists alike, albeit tainted in the minds of many by its association with Lamarckism. However, the social learning of knowledge, skills and vocalisation is now a well-established and non-controversial aspect of the adaptive behaviour of vertebrates. This social learning can take many forms, from social attraction to a location where individuals then learn independently (local enhancement) to the close observation and copying of the behaviour of a conspecific (imitation). The largest body of evidence for social learning comes from vocal learning studies of birds and foraging specialisations in primates and, in some cases, the patterns observed are evocative of human cultural variation. However, whether this resemblance is superficial, indicative of convergent selection acting on humans and animals, or a manifestation of homologous traits shared with humans, is highly contentious [1–5].

Debates have revolved around how to define culture, what kinds of social learning support it and how best to interpret behavioural variation [1–5]. Even for humans, culture has proven a difficult concept to pin down and there exists little definitional consensus within the social sciences. Whereas some researchers characterise species as cultural according to whether they exhibit 'key characteristics' of human culture, we suggest here that an anthropocentric perspective acts as a barrier to understanding the evolutionary roots of culture, and jeopardises our ability to see

relationships among culture-like phenomena in diverse taxa. A broad definition is likely to be more stimulating and henceforth we refer to culture (or tradition) as all group-typical behaviour patterns, shared by members of animal communities, that are to some degree reliant on socially learned and transmitted information [4]. Here, we criticize the dominant ('ethnographic') method for identifying animal cultures, which seeks to isolate cultural variation by ruling out alternative explanations for behavioural differences, and instead advocate a more thorough consideration of the interplay between genetics, ecology and culture.

Animal cultures

The idea that animals might acquire components of their behavioural repertoire by copying others has a long history, dating back to Aristotle. Several early evolutionists, including Wallace, Morgan and Baldwin, emphasised learned traditions as a source of adaptive behaviour [6]. More recently, researchers have documented vocal dialects in bird song [7] and the diffusion of novel foraging behaviour in animal populations [8–10]. Whereas some animal traditions might be specialised adaptations, a few animals (e.g. some primates) appear to have a broad cultural repertoire. For instance, building on earlier work of McGrew [1], Whiten *et al.* [11] synthesised behavioural information on chimpanzee *Pan troglodytes* populations collated from seven different sites across Africa. Their analysis revealed 65 categories of behaviour, 42 of which exhibited significant variability across sites. Some of this variation could be attributed to differences in ecology. For instance, the absence of ground night-nesting at four sites could be explained by high-predation risk from leopards and lions. However, once ecological explanations had been discounted, 39 variants, including tool usage, grooming and courtship behaviour, were absent at some sites but common at others, and it is these that Whiten *et al.* described as cultural. As in human societies, for which differences are constituted by multiple variations in technology and conventions, the behavioural profiles of each community were also distinctively different. Seemingly a unique case could be made for the chimpanzee as a cultural animal.

However, far from singling out chimpanzees, the study prompted a spate of articles arguing that geographical differences in the behavioural repertoires of other large-brained mammals were cultural [12–15]. The approach, commonly known as the 'ethnographic method' [16], has now become the standard means for detecting animal culture. For instance, van Schaik *et al.* [12] applied this method to six orangutan *Pongo* spp. populations

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throughout Borneo and Sumatra. The authors identified 24 putative cultural variants, including feeding techniques and social signals, with each population characterised by a distinctive repertoire; for example, some populations of orangutans make leaf-bundle ‘dolls’, whereas others use tools as sexual stimulants or blow raspberries at bedtime.

Around the same time as van Schaik *et al.* were writing [12], a long-term collaborative study of capuchin monkeys *Cebus capucinus* revealed behavioural variation in the social conventions of 13 social groups throughout Costa Rica [13]. Several striking and often bizarre social conventions were candidate cultural traditions, including hand sniffing, sucking of body parts and placing fingers in the mouths of other monkeys. Variation in such conventions is not obviously attributable to differences in ecological resource distribution across sites, and the monkeys might use group-specific social conventions to test the quality of their social relationships.

Social learning in cetaceans had also been established long before the recent flurry of studies of culture. Much of this research had been in the vocal domain of bottlenose dolphins *Tursiops truncatus* and humpback whales *Megaptera novaeangliae* [17] (Box 1). Calls and songs are more easily recognised as a form of social learning because communication signals can only be learnt from another animal. However, claims of social learning have been made for other domains, particularly foraging and migratory traditions, moving the topic of culture into the spotlight of cetacean research. A recent review [14] lists a broad range of traits that are interpreted to be cultural, including killer whales *Orcinus orca* beaching themselves during foraging and bottlenose dolphins foraging using sponges. In these species, variation in the expressed behavioural repertoires is comparable to that seen in primates.

Problems with the ethnographic method

Whereas advocates of animal cultures have argued that ecological and genetic factors, as well as individual learning, were unlikely explanations for intraspecific behavioural variation [1,11–15] other researchers strongly disagree [2,3,18,19], fuelling a vigorous and sometimes bitter debate. Although recent applications of the ethnographic method are an important step-up in the scale and rigour of cultural analyses, particularly through the systematic analysis of multiple geographical sites, the documenting of the absence of behaviour and recording variant frequencies [11,12], the approach suffers from major weaknesses. These separate into conceptual and interpretative problems.

Conceptual problems

Most fundamentally, the ethnographic method tries to demonstrate the influence of a factor (here culture) by excluding all alternative explanations (e.g. genetics, ecology or individual learning). This is a logical impossibility, because the absence of a cause cannot be demonstrated in any absolute sense. In this instance, it is impossible to rule out that some unknown ecological or genetic explanation explains the variance currently attributed to culture. Whereas practitioners claim that their efforts have established that the data are inconsistent with the presence of

Box 1. Vocal cultures

Vocal cultures can be found in numerous birds and mammals [7,17,38], and provide the largest body of evidence for cultural transmission of behavioural traits in the animal kingdom. However, vocal learning is still seen as a special adaptation [6,39,40] and it has not yet been fully integrated into discussions of animal culture. This is largely because early studies of bird-song learning stressed the importance of sensitive phases and the lack of flexibility once song had developed. Although this is true for some avian species (e.g. zebra finch *Taeniopygia guttata*), further work has revealed a remarkable variety of learning processes, including learning when to use a copied sound [41] and learning new song throughout life [7]. Thus, there are many birds that appear to be no more or less genetically predisposed to learn a song than a chimpanzee is to learn how to use a tool. There is a difference in that vocal learning does not occur in every avian species, whereas general associative learning can be found in all vertebrates. Although this is important if we are interested in learning mechanisms, it makes little sense to exclude vocalisations if we are looking at animal culture, just like it would make little sense to exclude spoken language from human culture studies. Bird and mammal dialect studies have given us a more detailed understanding of mechanisms involved in diffusion and cultural drift than have any other culture studies.

Studies of humpback whale *Megaptera novaeangliae* song demonstrate that studying culture is possible even with large and relatively inaccessible mammals, and provide some of the most compelling evidence for animal cultures (Figure 1). All males in a population share the same song at any one time, but the song changes gradually throughout the singing season. In Bermuda, humpback whales change, on average, 37% of their song each year, too rapid a rate to be explained plausibly by genes. It took 15 years to change the entire song [42]. However, off the east coast of Australia, the entire song changed within two years to match that found off the west coast [43], apparently triggered by the movement of a few individuals from the west to the east. Such cases can be used to investigate the meaning and mechanisms of cultural transmission.



Figure 1.

such unknowns, attempts to exclude other explanations are inevitably incomplete, because only a small proportion of genetic or ecological variables can realistically be considered.

Ironically, were the ethnographic approach to be rigorously applied, it would reject most genuine cases of culture. Correlations between behavioural and ecological variables are to be expected, because culture is a source of adaptive behaviour, enabling animals to learn about and exploit environmental resources. Similarly, cultural and genetic covariance is also anticipated, because much

animal learning is influenced by evolved predispositions and aptitudes. At the extreme, the reliance of the ethnographic method on ruling out alternatives would leave itself with little to explain.

Another conceptual problem is that the ethnographic method appears to have encouraged the treatment of behaviour as being genetic, ecological or cultural. This categorical thinking evokes memories of the nature–nurture debate, associated with polarised views long since rejected by behavioural developmentalists [20]. Clearly, genes, ecology and learning all influence vertebrate behaviour, and each explain some of the observed variation. Such influences might be subtle. Thus, to identify cultural variation, not only is it not sufficient to rule out the possibility that the variation in behaviour constitutes unlearned responses to different selection pressures, but it is also necessary to consider the possibility of genetic variation precipitating different patterns of learning. DeWaal [21] dismisses genetic explanations for chimpanzee behavioural variation on the grounds that ‘Genes determine general abilities, such as tool use, but it is hard to imagine how they instruct apes how exactly to fish for ants’. Yet even if we accept a vital role for learning in tool use by apes, it remains plausible that differences among ape populations might be caused by alternative genetic influences on learned behaviour.

Interpretive problems

There are also question-marks over claims that other factors can not explain ‘cultural variation’. For instance, Whiten *et al.* [11] sampled across two chimpanzee subspecies, *verus* at the western sites and *schweinfurthii* in the east, while van Schaik *et al.* [12] sampled two orangutan species in Borneo (*P. pygmaeus*) and Sumatra (*P. abelii*). Could some of this behavioural variation be genetic in origin? Seemingly, chimpanzee and orangutan primatologists have been reluctant to consider this possibility [11,12,21]. However, in the light of experimental studies of woodpecker finches *Geospiza pallida* and New Caledonian crows *Corvus moneduloides*, which revealed impressive tool use in birds reared with no opportunity to learn socially how to use tools [22,23], ignoring genetics might be ill-advised. A third of the chimpanzee ‘cultural’ variants are observed in one sub-species alone, and half of the orangutan variants are only seen in one of the two species. Some chimpanzee subpopulations have been genetically isolated for hundreds of thousands of years, and *verus* and *schweinfurthii* occupy distinct branches of a neighbour-joining tree based on genetic distances for mtDNA haplotypes [24]. Thus, it is plausible that some behavioural differences among chimpanzee sites have a genetic origin. There are similar concerns over the orangutan data, where a reported correlation between distance between sites and ‘cultural difference’ [12] might merely reflect the well-established correlation between genetic and geographical distances, and it is not clear that this association would hold if analyses were restricted to a single species.

Even if differences between sites covary with genetic differences, this does not rule out culture. Conceivably, chimpanzees and orangutans might have evolved predispositions to learn some associations more readily than

other associations, as is observed in rhesus macaques *Macaca mulatta*, who acquire a fear of snakes through observation of conspecifics, but cannot readily be conditioned to fear other objects [25]. Yet the detection of genetic covariates remains a serious problem for an ethnographic method that treats as cultural that variation in behaviour that remains after genetic and ecological factors have been excluded.

More compelling evidence for culture comes from variation within chimpanzee subspecies. Methods of phylogenetic reconstruction applied to both *schweinfurthii* and *verus* have revealed no statistically supported subdivision within subspecies [24,26]. Most candidate chimpanzee cultural variants differ in frequency among populations of the same subspecies, and these genetic analyses render a genetic explanation for these differences less plausible. Arguably, future applications of the ethnographic method to chimpanzees would be better restricted to a within-subspecies level.

Rendell and Whitehead [14] argued that genetic explanations for marine mammal culture were unlikely because there is a strong matrilineal component to the inheritance of behaviour. However, the pattern of inheritance for most ‘cultural’ variants is not established sufficiently reliably to rule out genetic inheritance. A report of sponge feeding in bottlenose dolphins [15] provides an illustrative example. Some dolphins at Shark Bay, Western Australia, are thought to use marine sponges as foraging tools, although the role of the sponge is still unclear. Using mtDNA analyses, Krützen *et al.* showed that most spongers belong to one matriline. Intuitively, this seems to imply genetic transmission but, after comparing the pattern of inheritance to several genetic inheritance mechanisms (including X- and Y-linked, autosomal dominant and recessive), the authors concluded this was unlikely. Krützen *et al.* report that it is almost exclusively females that sponge, claiming this does not fit a genetic explanation. However, of sexed dolphins that had been observed to use sponges at least once, 20% are male [27]. A genetic explanation might yet be plausible if adult males and females exhibit different patterns of foraging and habitat use. For instance, polygenic inheritance is possible if there is assortative mating among spongers, and although there was little evidence for this, the analysis lacked the statistical power to rule it out. Another interesting possibility in marine mammals is that variation in sponging might be a by-product of differences in energy budgets caused by genetic variation in mitochondrial efficiency. For instance, all dolphins might be capable of sponging if they had sufficient energy, but only those in lineages with high energy levels would regularly exhibit the behaviour. Because mtDNA is passed on maternally, this could result in the same phenotypic pattern as (maternal) cultural transmission.

Other critics believe that ecological differences explain the variation in putative cultures [2–4,28,29]. This ‘ecological explanation’ refers to cases in which behavioural variation reflects differential phenotypic plasticity, be it learned or unlearned, in response to ecological variation rather than to culture. Although Whiten *et al.* [11] consider the possibility of false positive reports attributable to an ecological explanation, only three of the 65 observed

behaviour patterns were removed because such an explanation could be given, leaving the critics questioning how seriously this alternative was considered [28]. This problem is highlighted by a recent analysis of chimpanzee ant-dipping [30], which found that different methods were used within a single chimpanzee population for different kinds of ant. Conceivably, chimpanzees at different sites could individually be shaped by biting insects to use the strategy that resulted in the fewest bites, with variation in chimpanzee behaviour a consequence of differences in ant aggression. Although the study does not rule out a cultural interpretation, it nonetheless puts the ecological explanation back in the frame.

Some researchers [14] have argued that ecological explanations can be disregarded for cetacean 'culture' because sympatric pods develop different behaviour. However, an ecological explanation could be viable if pods utilise the same habitat in different ways. In principle, social learning (or unlearned preferences) could explain pod ranging behaviour whereas ecological factors could explain variation in foraging. In bottlenose dolphins, it is possible that all dolphins have sponging in their repertoire but only those with extensive use of areas with sponges display the behaviour. Krützen *et al.* discard this argument by stating that four females regularly use the sponge channels but do not sponge. This is a small number of observations with which to dismiss ecological explanations, and it is likely that some individuals might fail to learn asocially to perform a tool-using behaviour in spite of exposure to the relevant ecological factors. Generally, there is a large difference between spongers and non-spongers in the amount of time that they spend in channels (B.L. Sargeant, PhD thesis, Georgetown University, 2005) and this implies that at least one ecological variable (channel use) strongly covaries with sponging.

Conclusions and future directions

We suggest that genetics and ecology could have more of an influence on reported cases of culture than was previously assumed. Favouring just one simple explanation is a by-product of an outmoded categorical perspective on behaviour encouraged by the ethnographic approach. Clearly, behavioural differences can simultaneously result from genetic, ecological and cultural variation. Sponging, ant-dipping and nut cracking are not genetic, learned or cultural traits, they are (probably) all three. Researchers studying animal culture would be better advised to think in terms of partitioning variance to alternative sources, rather than allocating behaviour to categories. The prime issue in the animal cultures debate is not whether a given behaviour is learned socially or asocially, but rather how much of the variance in the behaviour can be attributed to social learning. We anticipate that this change in focus would reveal significant interactions between genes, ecology and learning, including the interesting question of how cultural behaviour affects evolutionary processes (Box 2).

But what of the future? Are there new methods that could be used to identify cultural influences on behaviour and illuminate the animal cultures debate? Traditionally, social and asocial learning processes have been distinguished in

Box 2. How animal culture might affect evolutionary processes

Cultural processes present a challenge to biologists for several reasons. First, cultural transmission can cause the characteristics of the phenotype to become partially disconnected from its selective environment. Bluehead wrasse *Thalassoma bifasciatum* mating sites, for instance, cannot be predicted from knowledge of environmental resource distributions [33,34]. Second, akin to clines in gene frequency, cultural processes can generate geographical patterns in behavioural phenotypes, as described for ape behaviour, birdsong and cetacean calls [7,12,17]. Third, although cultural transmission typically propagates adaptive behaviour, both theory and empirical data suggest that arbitrary and even maladaptive variants spread in restricted circumstances. One such case is where it is costly for individuals to acquire information about resources, such as food or mates. Traditions might be Nash equilibria, in which it never pays any individual to abandon the tradition unilaterally, leaving populations locked into conventions that track changing environments inefficiently [44]. Another case is informational cascades, where individuals base behavioural decisions on the prior decisions of others [45]. Among lekking sage grouse *Centrocercus urophasianus*, the decisions of females using social information to decide with whom to mate were less closely correlated with male traits indicating quality than were the decisions of females making their own judgements about male characteristics [46]. Mate-choice copying will obscure the relationship between male quality and mating success, resulting in unpredictable 'fads' in the characters that females find attractive and a lowering of the intensity of sexual selection.

Fourth, cultural traditions might impact on the ecological or social environment to modify the selection pressures acting on the population, a form of niche construction [47]. This is most obvious in humans and a great deal of theory has investigated gene-culture coevolution [48]. In other animals, theoretical models of mate-choice copying reveal that learned preferences could plausibly coevolve with gene-based traits [49,50]; models of birdsong suggest that song learning affects the selection of alleles influencing song acquisition and preference [51]; and other analyses have found that song learning could lead to the evolution of brood parasitism and facilitate speciation [52,53].

Another possible example of gene-culture coevolution is 'cultural hitchhiking' in whales. Whitehead [54] notes extremely low nucleotide diversities in the mtDNA of four whale species. He suggests that this loss of variation has occurred through 'cultural hitchhiking', a process in which selectively advantaged and matrilineally transmitted cultural traits sweep through a population, dragging neutral mtDNA alleles to fixation. Although there are other explanations for low genetic variation in these species [55], Whitehead's hypothesis remains an intriguing possibility.

the laboratory in paired demonstrator-observer designs [6], but such experimentation is usually impractical in natural contexts. Moreover, a capacity for social learning is merely a prerequisite for culture. Laboratory and captive animal studies have successfully investigated the diffusion of learned behaviour through populations, or along chains of animals in a Chinese-whispers-like design [10,31]. However, although such studies shed light on social transmission processes and the capabilities of particular species, at best, they provide circumstantial support for the argument that natural behaviour is cultural.

One promising avenue is the use of field experiments, such as translocations of individuals between populations, or of populations of animals between sites, which could, in principle, distinguish between alternative explanations [4]. For instance, if newly introduced animals adopt the behaviour of established residents, this is inconsistent with an explanation in terms of genetic differences



Figure 1. Bluehead wrasse *Thalassoma bifasciatum*. Some of the strongest experimental evidence for animal culture is found in fishes. Removal and translocation experiments of populations of bluehead wrasse reveal that their mating sites cannot easily be predicted from knowledge of the local ecology [33,34]. Rather, they appear to be maintained as local cultural traditions, with youngsters and newcomers learning the routes to sites from experienced residents. Reproduced with permission from Kenneth Clifton.

between populations. Similarly, if an entire population is replaced, and the introduced individuals come to exhibit the same behaviour as the former inhabitants, this would suggest that the variation results from adjusting to divergent ecological conditions. The approach has been used successfully to demonstrate culture in fishes [32–34] (Figure 1) and could be applied more widely. Although this method is neither feasible nor ethical in many species, particularly apes, it might nonetheless be possible to exploit natural movements of animals between populations, or exchange of captive animals between holding facilities, to draw similar inferences.

Methods are starting to emerge for differentiating socially contingent learning from asocial learning in animal populations. For instance, socially contingent learning should generate a greater than expected homogeneity in the behaviour of individuals in a population, as they learn from each other. Researchers could bootstrap probability distributions for the asocial learning of a target behaviour, either based on the measured performance of isolated captive animals or, for tasks with two or more alternative solutions (options), based on the computed probability of levels of homogeneity (option biases) of the observed magnitude (R.L. Day, PhD thesis, University of Cambridge, 2003). Social learning can be inferred if the observed level of behavioural homogeneity is extreme relative to a sampling distribution based on asocial learning, with asocial learning and chance performance rejected at the $p = 0.05$ level.

Another method identifies statistical ‘signatures’ of cultural transmission, namely, rates, pathways and patterns of spread, that will rarely be associated with exclusively asocial learning but are diagnostic of social learning. Whereas some attempts have been discredited [35,36], such analysis is at a formative stage and it is likely that social-learning signatures will eventually be identified. Finally, researchers can develop mathematical models of asocial and social learning and fit these to behavioural data. This approach was used to analyse the spread of

novel foraging behaviour in callitrichid monkeys, finding evidence for some social learning processes [37]. Although all these methods are very much in their infancy, they exhibit sufficient promise to hint of a future resolution to the animal cultures debate.

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